Fig. 5. *Cypris Verreauxii*, on its side, magnified 20 diameters; 5 *a*, the same, seen from underneath, magnified 20 diameters.

Fig. 6. *Cypris Yallahensis*, on its side, magnified 40 diameters; 6 *a*, the same, seen from underneath, magnified 40 diameters, with natural size annexed.

II.—*On the Systematic Position of the* Charybdeidæ.

By Fritz Müller*.

Eschscholtz's section of the *Discophoræ phanerocarpæ* formed a well-defined group of closely allied animals, united by a great number of common characters:—the disk a shallow and smooth segment of a sphere, but capable of being more strongly arched during natation, with a notched margin, in the notches of which, always to the number of eight, are the marginal corpuscles with crystals insoluble in acids; round the mouth four arms, and alternating with these, in peculiar pits, the sexual organs, forming bowed bands folded like frills; the stomachal filaments in the same place, and so forth. The mouth, indeed, was sometimes freely open (*Medusidæ*) and sometimes closed, and, instead of it, numerous orifices on the arms (*Rhizostomidæ*); but this peculiarity of the *Rhizostomidæ*, important as it certainly is for their mode of obtaining nourishment, did not disturb the morphological unity of the group, as it is derived without difficulty from the ordinary form of mouth †. Some subsequently discovered somewhat anomalous forms of *Medusidæ* likewise did not prejudice the unity of the general picture, which they only served to complete‡.

* Translated from Wiegmann's 'Archiv,' 1861, by W. S. Dallas, F.L.S.

† Gegenbaur (Zeitschr. für wiss. Zool. viii. p. 210, note) declares the polystomism of the *Rhizostomidæ* to be a paradox not reconcilable with the general plan of the *Medusæ*, and even doubts the fact. The fact is easily ascertained, and has lately been repeatedly proved, even by myself. Its explanation also seems to me to be pretty easy. A temporary polystomism, if it may be so called, may be easily seen in Hydroid Medusæ, where the margins of a much-folded four-lobed oral fringe lie upon each other here and there. Thus also the polystomism of the *Rhizostomidæ* will result from the growing together of the membranous laminæ which surround the arms of the *Phanerocarpæ*. When the orifices of the arms have the form of long slits, often continued into strap-like tentacles, as in a *Cephea* of the South-Brazilian coast, scarcely any doubt can remain as to this mode of production. It seems more difficult to explain the perforation of the peduncle of the arms, or its "origin with four roots," as occurs in the same *Cephea*, and, according to Forskal, in *C. octostyla*.

‡ Such as *Nausithoë*, Köll., with its eight extremely simple sexual glands, and *Trichoplea*, u. g., with marginal corpuscles in deep niches on the under surface, two inches from the undivided margin of the disk, which measures two spans in diameter. Amongst the older, less accurately-known species, *Medusa persea*, Forsk. (*Rhizostoma*, Eschsch.), is certainly to be placed with the "*Acraspeda*," notwithstanding its undivided margin and large velum.

It is otherwise, however, with the family of the *Charybdeidæ*, which Gegenbaur arranged with his Acraspeda, the Phanerocarpæ of Eschscholtz. *Charybdea marsupialis*, Péron, and still more *Tamoya haplonema* and *T. quadrumana*, described by me, are opposed most decidedly in almost all the essential features of their structure to the above general picture: a bell with deeply furrowed sides and a broad velum, scarcely capable of any alteration of form; the marginal corpuscles four in number, distant from the margin, in deep niches of the outer surface of the bell; a long oral funnel, after the fashion of *Thaumantias*; sexual organs in the form of broad membranous laminæ in the wide lateral pouches of the stomach, and therefore remote from the stomachal filaments; tentacles upon peculiar clavate or hand-like processes; a distinctly marked nervous system, &c.

In its external form (and this only is known) the *Charybdea periphylla*, Péron, is almost still more strikingly in contrast to the ordinary *Medusæ*; it is, as it were, a *Tamoya quadrumana* with hand-like appendages increased to sixteen in number, and deprived of their tentacles.

It appears, therefore, scarcely possible to imagine transition-forms between the *Charybdeidæ*, on the one side, and the *Medusidæ* and *Rhizostomidæ*, on the other, or even to derive the two groups from a common fundamental form containing essentially anything more than the general features of all *Hydromedusæ*. The intuitively clear picture of Eschscholtz's *Phanerocarpæ* would fade into a shadow by the reception of the *Charybdeidæ*, and at any rate their union would be perfectly unnatural.

And yet, if we will retain the usual bipartition of the Discophorous Acalephs, in which the systems of Forbes, Lütken, and Gegenbaur have altered nothing but the names*, and which even recurs (in respect of the Medusoid forms) when the *Discophoræ*, and rightly, are no longer recognized as a systematic unity, as in the *Acalephæ* and *Hydroida* of R. Leuckart, the *Charybdeidæ* can only find a place among the higher *Medusæ*, with which they have in common at least the stomachal filaments and the insoluble contents of the marginal corpuscles. It cannot be disputed that they are still further removed from the Medusoid brood of the *Hydroida*.

On a former occasion, in describing the *Tamoyæ*, I already thought of a preferable tripartition of the *Discophoræ*, and anti-

* Not the foundation, or principle of division, as Gegenbaur will have it. Eschscholtz by no means regards the "germ-cushions" as either the sole or most important character of the Phanerocarpæ: he placed, like Gegenbaur, the emargination of the margin in the first rank, and was very well acquainted with "the soft, membranous, annular lobe on the margin of the disk," as the common character of his Cryptocarpæ.

cipated that this would derive support from the developmental history. Still earlier, although information of the fact did not penetrate to the place of my exile until subsequently, R. Leuckart, following the same idea, had formed the section of *Ceratostera*, but soon gave it up again; for his supposition has, as is well known, proved to be quite destitute of foundation. Krohn saw *Pelagia noctiluca* reproduce without change of brood, whilst Busch traced the brood of *Chrysaora*, which is scarcely separable generically from *Pelagia*, up to the polype-form. Among the *Hydroida*, it has been shown by Gegenbaur that *Trachynema ciliatum*, and by myself that *Geryonia* (*Liriope*) *catharinensis*, are probably developed directly from the egg; whilst, on the contrary, the supposition of the direct evolution of the *Æginidæ*, founded solely upon the ciliary coat of the young of *Æginopsis*, has lost its support by the discovery of ciliated brood in the stomach of *Cunina Köllikeri*.

Nevertheless, my formerly imagined grouping of the *Discophoræ* has become more and more plausible with every new investigation. It appears to me that in this case, as in so many others, the unfettered intuition of the older observers has hit the right course in uniting with *Charybdea marsupialis* and *periphylla* the *Charybdea bitentaculata*, which is now usually placed, under the name of *Æginopsis mediterranea*, J. Müll., or *Æ. bitentaculata*, Köll.*, in the family *Æginidæ*, at the end of the *Cryptocarpæ*. Not that I would support the union of *Charybdea* and *Æginopsis* in the same genus, or even, after the example of Lütken, in the same family; but I am of opinion that *the families* Charybdeidæ *and* Æginidæ, *Ggbr., are to be united to form a group of the* Hydromedusæ *equivalent to the* Siphonophora, Hydroida, *and* Acalephæ (in Leuckart's sense). To group together the most highly organized of all known Hydromedusæ, and perhaps of all Cœlenterata, the *Tamoya quadrumana*, and the *Æginidæ*, which apparently represent the lowest step in the series of Hydromedusæ, and some of which, such as *Eurystoma*, Köll., only digest by the cavity of the lower surface, which is partially closed by the velum†, certainly long appeared to me to be rather a doubtful course. Since I have been able to examine carefully a species extremely similar to this *Eurystoma* both in form

* The difference of colouring can hardly be accepted as a specific distinction in a group of animals in which, as in the Acalephæ (*Rhizostoma*, *Chrysaora*, &c.) and Hydroida (*Corymorpha*), the greatest variability of coloration within the species may almost be regarded as the rule.

† I did not think I might doubt this representation of Kölliker's (which is probably erroneous) upon Gegenbaur's authority alone, as in other *Medusæ* I had not always found his statements perfectly well founded,—still less on account of any *à-priori* notions respecting "a general plan of the Medusæ."

and in the development of the brood budding in the stomach, and since I have again obtained Eschscholtz's admirable 'System der Akalephen,' this hesitation has disappeared; and I now regard my view as sufficiently well founded to venture to submit it to the judgment of zoologists.

The incompatibility of the *Charybdeidæ* with the Acalephæ of Leuckart has already been spoken of. *Cunina*, *Æginopsis*, and their allies stand in a precisely similar position towards the other Cryptocarpæ or Hydroid Medusæ. The disk of the latter, although very variable in form, is still always entire at the margin, and either smooth, as in the other Acalephs, or furnished with slightly projecting ridges running from the middle of the back; they have always radiating vessels and an annular canal, and the former, except when very numerous, in a fixed number; the marginal vesicles, when present, are always roundish and sessile; the marginal filaments, although very variable in structure, always occupy the immediate vicinity of the annular vessel. Lastly, in the structure of the sexual organs, the Hydroid Medusæ approach the Acalephæ (Leuckt.) or Phanerocarpæ; for, although their forms are exceedingly numerous, the extremes are united by a tolerably close series of intermediate forms (from the astomatous sexual clubs of the Medusæ of *Corymorpha* to the densely appressed ramifications along the radiating vessels of *Olindias**), they still always occupy the external wall of the gastrovascular system, and empty their products externally. On the other hand, the disk of *Cunina* and its allies is frequently, if not always, notched at the margin†, and, as in the *Charybdeidæ*,

* *Olindias*, nov. gen. Habitus of *Thaumantias mediterranea*, Ggb.; four radiating vessels, and numerous (more than 100) retrograde vessels; at the margin extremely extensible filaments and slightly moveable tentacles, both hollow and of indefinite number; at the base of the tentacles are the marginal vesicles in pairs; the sexual organs are arborescently ramified along the radiating vessels. It is probable that the filaments (*Fangfäden*) on the radiating vessels of *Melicertum* are nothing but sexual organs, and this the rather, as even in the structure of the marginal filaments *Olindias* approaches most closely to *Melicertum*. As a transitional structure from the stomachal to the peripheral sexual organs, I may cite, not to refer to undescribed forms, *Lizzia Köllikeri*, in which, according to Gegenbaur's observation, confirmed by me on a nearly allied species, the sexual gland lying on the stomach is traversed by a branch of the radiating vessel.

† Gegenbaur is of opinion that the possession of a velum presupposes an entire margin of the body, and for this reason, apparently, he denies, in opposition to Eschscholtz and Kölliker and in contradiction to himself, the notching of the margin in the *Æginidæ*; for in *Ægineta flavescens* he shows the gelatinous substance continuing itself in considerable thickness upon the stomachal sacs; in the intervals, therefore, there are gaps or notches of the gelatinous substance, *i. e.* "the body," over which only membrane is stretched; as in the *Æginidæ*, which are destitute of an annular vessel, only the cessation of the gelatinous substance can indicate

traversed by deeper or shallower furrows, extending a greater or less distance upon the dorsal surface; the stomach has broad lateral sacs, often in variable number, no radiating vessel or annular canal; the marginal vesicles are usually pedunculate; the tentacles, never exceeding the number of the stomachal sacs, are always situated on the back, often springing very far from the margin; they are, moreover, characterized sometimes by a peculiar rigidity, and sometimes by "a mobility not observed in other Medusæ" (Eschscholtz*). The sexual materials of *Cunina* are formed in the interior of the lateral sacs, and, indeed, in their lateral angles, from which their place of formation extends in the form of a horse-shoe from one sac to another.

From all this, the alliance of *Cunina*, *Æginopsis*, &c. with the Hydroida is equally loose and forced, and as little effected by any transitions as that of the *Charybdeidæ* with the Acalephæ. If, therefore, the separation of these two families from their present alliances is not subject to any serious doubt, neither does any such appear to present itself against their union. It is true that a wide gap exists between *Cunina* and *Tamoya*, but not wider than between the Medusoid of *Corymorpha*, without tentacles, eyes, or mouth, and *Olindias*, or between *Nausithoë* and *Cephea*—a gap like that between the young brood and the mature animal, over which fancy readily finds a gradual passage by intermediate steps, and not a wall of separation set up by incompatible characters. From the shallow furrows in the flat, slightly notched disks, often (according to Gegenbaur) of a cartilaginous hardness, of many *Cuninæ*, the intermediate form of *Æginа citrea* leads to *Charybdea marsupialis*, and to the complex bells of the *Tamoyæ*, whilst, even in both the extreme genera, the combination of a velum with a disk not entire at the margins, observed neither in Hydroida nor in Acalephæ, occurs as a common character. From the flatly stretched stomachal membrane

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the boundary between body and velum. As in the *Æginidæ* the muscular membrane of the lower surface is continued over a notched margin, the marginal membrane may, in like manner, be wanting in disks with entire margins, even in Hydroid Medusæ; at least, I am unable to detect any trace of it in a small *Campanularia*-bud, *Tintinnabulum resupinatum*, n. s., which *always* swims with the disk reversed.

* This is the case in *Æginа sulfurea*, as it is called in Eschsch. System p. 9, or *Æg. citrea*, at p. 113. The second Eschscholtzian species, *Æginа rosea*, is probably to be separated from this, and referred to *Cunina*, as, according to Eschscholtz's figure (tab. x. fig. 3 *a*), it appears more natural to ascribe to the stomach six lateral sacs excavated opposite to the origin of the tentacles, than twelve such organs. If, with Gegenbaur, we characterize the *Æginidæ* by "rigid tentacles," the choice of the name after that of a species distinguished from all other Medusæ by the exact opposite cannot be described as particularly happy.

of *Cunina*, with its simple proteiform mouth, closely repeated in *Æginета*, *Polyxenia*, and *Æginopsis bitentaculata*, the four arms on the mouth of *Æginopsis Laurentii*, Brdt., lead to the structure of the stomach in *Charybdea* and *Tamoya*. In the same way the form of the sexual organs of *Tamoya* may be deduced without constraint from those of *Cunina*; but neither the one nor the other can be referred to the fundamental form developed in Hydroida and Acalephæ. If *Tamoya quadrumana* has an entire series of perfectly new parts not even indicated in *Cunina*, such as a well-developed nervous system, there is nothing remarkable in this; some of them, such as the eight finger-like processes in the base of the bell and the dendritic glands, are totally wanting even in *T. haplonema*.

The formation of the marginal corpuscles is certainly essentially different; but we still know nothing about their development in *Charybdea* and *Tamoya*, or of their structure in the intermediate forms *Ægina citrea* and *Æginopsis Laurentii*; and, again, their difference is not more considerable than between the eye-spots and marginal vesicles of the Hydroida.

The formation of the tentacles also is perfectly anomalous, but nevertheless by their dorsal origin they contrast equally with the marginal filaments of the Hydroida and Acalephæ. The tentacles of *Cunina* are rigid, those of *Tamoya* contractile; but those of the young brood of *Cunina* are also contractile. The tentacles of *Cunina* are solid, those of *Tamoya* hollow; but hollow and solid tentacles are exhibited by otherwise very nearly allied genera, such as the various *Campanularia*-buds*; nay, both forms occur simultaneously or successively in the same animal (*Liriope*). In this, therefore, no ground for the union of our two families can be sought; but that which especially speaks in favour of it is that at present it is not possible to draw a marked boundary-line between the two, and to refer the median forms

* For the *Campanularia*-buds with solid and but slightly moveable tentacles, exactly like those of *Campanularia* itself, I propose to retain Dalyell's name *Tintinnabulum*; it appears that they are always born with a greater number of tentacles. Here belongs also *Eucope polystyla*, Ggb. What Gegenbaur describes and figures in this species as roundish inflations of the annular vessel, directed into the substance of the disk, may be the thickened roots of the tentacles, judging from the nearly allied *Tintinnabulum resupinatum*, n. sp. The *Campanularia*-buds with hollow filaments dilated at the base and very contractile, of which, when set free, they have only four and the first traces of four more (*Eucope*, Ggb., excl. *E. polystyla*), have, in my opinion, a title to the name of *Thaumantias*; for it appears to me scarcely doubtful that it is to these, and not to *T. mediterranea*, Ggb., that the two Eschscholtzian species of *Thaumantias* belong; and for them, therefore, in a division of the genus, the old name should be retained.

to one or the other. Amongst these are *Ægina citrea*, which approaches the higher forms in the four arms and the great mobility of the tentacles, and *Æginopsis Laurentii*, which allies itself to them by the four arms at the mouth. So also *Charybdea periphylla*, Péron, which resembles *Tamoya quadrumana* in the form of the marginal appendages, but departs from the other *Charybdeidæ* in the multiplicity of its tentacles.

I would consequently arrange the *Charybdeidæ* in the following manner in the system of the Hydromedusæ :—

HYDROMEDUSÆ.

1. Siphonophora, including the free sexual animals (*Chrysomitra*).
2. Hydroida.
   a. *Tubularinæ*, together with the Hydroid Medusæ without organs of sense or with eye-spots.
   b. *Sertularinæ*, with the Hydroid Medusæ with marginal vesicles*.

   In respect of the development, there are in this group—
   α. Polypes without free sexual animals.
   β. Polypes with free sexual animals.
   γ. Free sexual animals without polypes (*Trachynema*, *Liriope*).
3. Acalephæ, R. Leuckt. (*Discophoræ phanerocarpæ*, Esch.).
   a. *Monostomatous* (*Medusidæ*, Esch.).
   b. *Polystomatous* (*Rhizostomidæ*, Esch.).
4. Æginoidæ (*Æginæ*, Lütk.).
   a. *Lower*: *Cunina* (with *Ægina rosea*, Esch.), *Ægineta*, *Polyxenia*, *Æginopsis bitentaculata*.
   b. *Higher*: *Charybdeidæ*. *Æginopsis Laurentii*?, *Ægina* (*citrea*), *Charybdea* (*marsupialis*), *Tamoya*, *Periphylla* (*C. periphylla*, Pér.).

* Gegenbaur was the first, as far as I know, who pointed out the importance of the ocelli and marginal vesicles in the Hydroid Medusæ, and laid some stress upon the difference of the marginal filaments; and, indeed, the families of "Craspedota" established by him, from being more natural and depending less upon the exclusive application of one character, contrast very advantageously with those of Forbes, and even of Lütken, and may serve as a more convenient starting-point for further systematic attempts. To future workers I would especially recommend a careful consideration of the marginal filaments, by which, apparently, amongst other things, the *Geryonidæ* and *Thaumantiadæ* of Gegenbaur might be more sharply defined.